Chapter 4

Nitrogen Deposition Mostly Predicts Gross Primary Production Response in Swiss Croplands, Grasslands, and Natural Vegetation Mosaics

This chapter is based on:

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Abstract

Gross primary production (GPP) is a key indicator of carbon (C) fixation that can be stored either as biomass or as soil organic carbon. Climate, soil type, and management practices have been reported as the main limiting factors of GPP. However, the extent to which these factors explain GPP variance is different among land cover classes and regions. Remotely sensed GPP products as well as climatic and recently available nitrogen (N) deposition datasets for the years 2000, 2007, and 2010 in Switzerland bring along the opportunity of studying GPP variance at large scale. We carried out stepwise multiple linear regression analyses between GPP (dependent variable) and N deposition, precipitation, relative sunshine duration, and temperature (regressors: independent variables and covariates) stratified per land cover class. Land cover classes were derived from the MODIS MCD12Q1 land cover product. We used the legend defined by the International Geosphere and Biosphere Programme (IGBP). The selected land cover classes were: grasslands, croplands, and croplands/natural vegetation mosaic characterised by low, high, and medium management practices respectively. Regression models generated with the selected explanatory variables explained up to 80% of the GPP response in grasslands. However, the explanatory performance of these variables decreased to a relative maximum of 47% in croplands, and 19% in croplands/natural vegetation mosaic. In all, N deposition mostly explained GPP variance (from 14% to 68%) in all land cover classes. Finally, we suggest monitoring the influence of N deposition rates in species rich plant communities and further inclusion of this variable in C budget models.

Keywords: gross primary production, agroecosystems, climatic factors, nitrogen deposition, carbon fixation, models.

4.1 Introduction

Organic carbon provides the quality required in agricultural soils to obtain high yields and foster food security (Lal, 2004a). Carbon (C) is fixed through photosynthesis and remains stabilized as new plant biomass (≈70%) until it is transferred to the soil (20-30%), released again to the atmosphere, or lost because of harvesting (Johnson et al., 2006; Lorenz, 2013; Lorenz et al., 2012). The total gross C fixed per unit of ground and time is known as gross primary production (GPP) (Chapin III et al., 2006). Most of the C fixed can be lost via autotrophic respiration (AR) —$C0_2$ released by primary producers (Lorenz et al., 2012). The subtraction of AR from GPP results into net primary production (NPP) (Chapin III et al., 2006).

The largest fluxes of GPP at a global scale are observed in the tropics, subtropics, and humid temperate regions e.g. Eastern North America, Western and Central Europe (Anav et al., 2015). Switzerland is located in one of the world regions (Western Europe) with the highest cultivated NPP (> 1 Kg C/m^2) (Monfreda et al., 2008). There are two large soil organic carbon (SOC) pools in agricultural soils, one located in areas with intensive agricultural management (200-700 m above sea level, a.s.l.) and the other found in extensive permanent grasslands (1500-3000 m a.s.l.) (Leifeld et al., 2005).

Climate, soil type, and land management have been pointed out as important factors influencing C sequestration in agriculture (Freibauer et al., 2004; Lal, 2004b; Smith, 2004). Precipitation has been reported as the climatic component with the highest impact on the primary production of croplands and temperate grassland biomes (up to 50 and 70% of the total area respectively) (Beer et al., 2010). Alternatively in agricultural regions with homogeneous climatic patterns, management practices can explain up to 70% of the SOC variability (Van Wesemael et al., 2010). In more extreme environments like (sub-)alpine areas (1500-300 m a.sl.), scientists have highlighted temperature, grazing, presence of rocks and stones, shallow soils, and nitrogen (N) deposition as the most limiting factors for biomass production and C storage (Bassin, Volk, Suter, et al., 2007; Hitz et al., 2001; Leifeld et al., 2009). Results of recent studies carried out in similar temperate grasslands indicate that water availability in conjunction with

N deposition can enhance GPP (Guo et al., 2016) as well as produce no effect on above ground biomass (He et al., 2016). Although N deposition likely enhances plant growth in low productive areas such as alpine grasslands, long-term ecosystems exposure to high N deposition quantities increases net C losses (Volk et al., 2011). Therefore, study the effects of this variable on C fixation response is crucial to understanding C and N cycles. Moreover, model simulations have shown the importance of coupling N and C cycles in order to improve global patterns of C and N fluxes and to better account for vegetation dynamics (Smith et al., 2014; Zaehle et al., 2010).

Remotely sensed GPP datasets are available to study C dynamics of land cover at global and regional scales (Running et al., 2004). GPP tends to be overestimated at low production sites and underestimated at high production areas (Turner et al., 2006; Turner et al., 2003). However, different validation efforts and following improvements in the algorithms have enhanced the reliability of remotely sensed GPP products for multiple applications (Turner et al., 2005; Zhao et al., 2005; Zhao et al., 2006). In particular, these products are suitable to study the production of land vegetated areas (Heinsch et al., 2006). Additionally, climatic datasets and recently available N deposition maps for Switzerland bring along the opportunity to account for the impact of these limiting factors on GPP response at large scale. In 2010, critical loads (threshold below which negative environmental effects do not occur according to present knowledge) of N deposition were exceeded in most of the Swiss forest and semi-natural ecosystems (Rihm et al., 2016). According to eutrophication criteria, N deposition quantities do not met Swiss sustainable goals. The highest exceedances occur in the lowlands where intensive management practices lead to high ammonia emissions because of high manure inputs (Rihm et al., 2016). This could have an additional negative effect in intensively used areas where N hotspots can be found (Gómez Giménez et al., 2017). The use of these datasets can contribute to a quick assessment of the impact of different factors on land productivity at large scale.

The aims of this study are: i) evaluating the influence of limiting factors of C fixation reported in experimental and field studies on remotely sensed GPP response; ii) analysing which factors are more relevant to controlling the GPP response in land cover classes. In order to understand differences in the role of limiting factors of C fixation per land cover class, soil characteristics such as aptitude for croplands, stone content, and water and nutrient storage capacity were analysed to determine the potential land management. The studied limiting factors are: precipitation, temperature, relative sunshine duration, and N deposition. The selected land cover classes are: grasslands, croplands, and croplands/natural vegetation (Friedl et al., 2010).

4.2 Methods

4.2.1 Study area

Switzerland is divided in biogeographic regions according to flora and fauna patterns (FOEN, 2004), (Figure 4.1). The classes derived from the land cover MODIS product (MCD12Q1) croplands and croplands/natural vegetation mosaic, are mostly found in the Midlands and the Jura mountains. The class grasslands, which is also obtained from the MODIS land cover product, is mainly located in the Alps. The Midlands is a heterogeneous floristic region with an altitudinal range between 256 m and 960 m a.s.l. (Gonseth et al., 2001). The Alps and the Jura mountains have significant altitudinal gradients affecting climatic patterns such as precipitation, temperature, and sunshine. According to the Digital Height Model (Swisstopo, 2015), the altitudinal range in the Alps is between 193 m (Southern Alps) and 4629 m a.s.l., (Western Alps). In the Jura, altitudes are between 272 m and 1677 m a.s.l. In mountainous areas, pastures co-exist with extensively managed fields characterised by low yields and high plant species diversity (Kampmann et al., 2008). According to the Digital Height Model (Swisstopo, 2015), the land cover classes selected can be found from minimum altitudes ca. 200 m to maximums of 2634 m a.s.l., in croplands, 3033 m a.s.l., in croplands/natural vegetation mosaic, and 3570 m a.s.l., in grasslands.

The Swiss climate is influenced by the Atlantic Ocean with an average precipitation ca. 2000 mm/year in the Alps and 1000-1500 mm/year in lowlands. The Alps divide the country producing cooler temperatures in the North than in the South, which is influenced by the Mediterranean Sea. Temperatures are influenced by altitude ranging from 1 °C in winter to 17 °C in

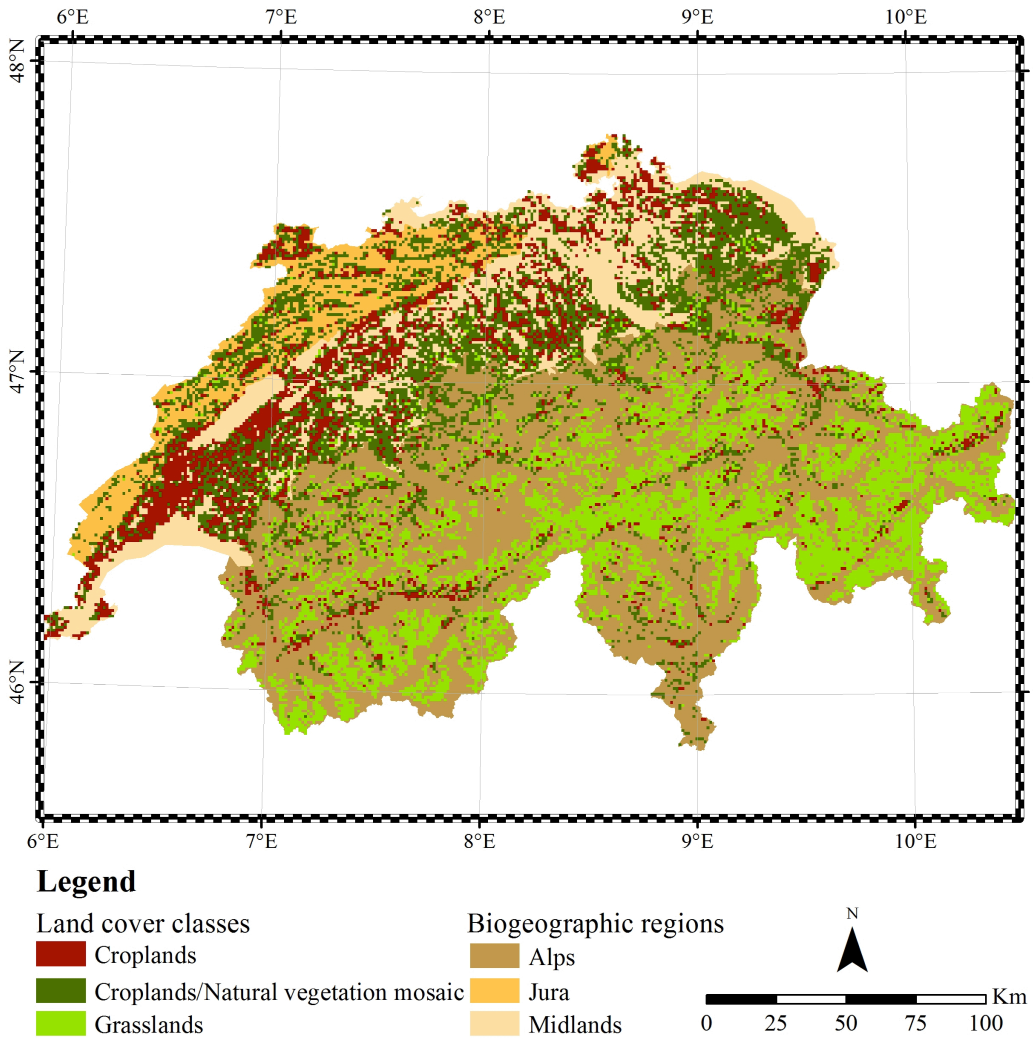

Figure 4.1 Study area. Land cover classes distributed across (aggregated, e.g., Alps) biogeographic regions are shown. Coordinate system: WGS84 UTM 32N.

summer at low altitudes (<1000 m a.s.l.), from -5 °C in winter to 11 °C in summer at 1500 m a.s.l., and annual means of -7.5 °C at altitudes above 3000 m a.s.l. (Meteoswiss, 2014). The Midlands receive more relative sunshine than the Alps and the Jura (Meteoswiss, 2015a).

4.2.2 Data

4.2.2.1 MODIS datasets

8-day GPP composite products (MOD17A2 version 5.5) for the years 2000, 2007, and 2010 were used in this study (Running et al., 2000). These years were selected for comparison with available N deposition datasets. An annual product was derived (by addition of composite values) and flagged data were filtered out. The land cover classes were obtained from the MODIS product MCD12Q1 (Friedl et al., 2010). The International Geosphere and Biosphere Programme (IGBP) defined a legend with 16 classes. The classes 10, 12, and 14 were selected i.e., grasslands, croplands, and croplands/natural vegetation mosaic respectively. All datasets were used at a spatial resolution of 1 km.

4.2.2.2 N deposition datasets

N deposition raster datasets for the years 2000, 2007, and 2010 were used with a spatial resolution of 1 km (FOEN, 2016). In particular, N deposition maps have been retrieved following a modelling approach based on wet and dry deposition of nitrate and ammonium, and gaseous deposition of ammonia, nitrogen dioxide, and nitric acid. Combustion processes and agricultural activities, in particular those related to livestock such as application and storage of manure, housing, and grazing, are the main sources of these atmospheric components. Further details can be found in Rihm et al. (2016). For this study, dry and gaseous depositions were calculated only for low vegetation (excluding forest stands).

4.2.2.3 Weather datasets

We used gridded datasets of annual mean values of temperature, yearly-accumulated precipitation, and yearly relative sunshine duration (the ratio between the effective sunshine duration and the maximal possible) for the years 2000, 2007, and 2010 with a spatial resolution of 2.3 km (Meteoswiss, 2013). Weather datasets were downscaled to 1 km in space and time, allowing comparison with all other data.

4.2.3 GPP response to limiting factors per land cover class

Multiple linear regressions models were built for the years 2000, 2007, and 2010 according to the spatial extension of grasslands, croplands, and croplands/natural vegetation mosaic. A sample with unique values was randomly selected in order to avoid oversampling. Cook's distance (4/n, n: number of samples) helped exclude outliers and values producing leverage. GPP was used as dependent variable and as regressors (independent variable and covariates): precipitation, temperature, sunshine, and N deposition. Linear relationships between the dependent and independent variables were checked using Pearson's correlations and scatterplots (data not shown). A forward stepwise model was selected to include the regressors in the model. The model selected the order of entry according to the correlation between the independent variable and the dependent variable. The independent variable with the highest correlation with the dependent variable entered the model first. Then, the rest of the explanatory variables entered into the model automatically according to their correlation with GPP and, as long as the default tolerance threshold (0.0001) of collinearity between the explanatory variable already in the model and the new entered one was not exceeded. The probability of the model to select an explanatory variable was also defined by an entry criteria with a threshold of $p < 0.05$ and a removal criteria with a threshold of $p > 0.1$. These criteria helped include variables in the model increasing the R^2 with changes statistically significant. Collinearity statistics determine dependence between regressors. Results were interpreted following the rule of thumb of no collinearity whether tolerance ($T = 1 - R^2$) was less than 0.1 and variance inflation factor ($VIF = 1/T$) was higher than 10 (IBM Corp., 2012; Midi et al., 2010).

Independence of residuals was analysed with the test Durbin-Watson (D-W). D-W ranges from 0 to 4, with values equals 2 indicating no correlation. Normal distribution of the standardized residuals was checked with P-P plots and histograms (data not shown). Homoscedasticity was analysed with two tests, namely Breuch-Pagan (B-P) and Koenker (K). The latter was used in case of non-normal distribution of standardized residuals. In case the assumption of homoscedasticity was violated, heteroscedasticity-consistent (HC) standard errors were estimated (Darlington et al., 2016). The HC4 estimator was used for all the cases because of high performance in case of high leverage or non-normal distributed errors (Hayes et al., 2007). Finally, we estimated the shrunken (SR) R^2 with a leave-one-out cross-validation approach for statistical inference from our regression models (Darlington et al., 2016).

4.2.4 Soil characteristics per land cover class

The digital soil suitability map for Switzerland was generated in the 1970's at a scale of 1:200'000 using spatial information regarding geology, elevation,

Table 4.1 Classes selected of the soil suitability map divided in levels.

Class	Aptitude for croplands	Stone content	Water storage capacity	Nutrient storage capacity
1	Very good	Not stony	Extremely low	Extremely low
2	Good	Slightly stony	Very low	Very low
3	Medium	Stony	Low	Low
4	Limited	Very stony	Medium	Medium
5	Inappropriate	Extremely stony	Good	Good
6		Unknown	Very good	Very good
7			Unknown	Unknown

terrain attributes, and climatic zones. This map was used to characterise the selected land cover classes in terms of soil aptitude for croplands, stone content, and water and nutrient storage capacity (Table 4.1), (FOAG, 1980). The soil suitability map was converted to a raster layer with a spatial resolution of 1 km. The value of the polygon that overlapped the centre of the raster cell was used to assign the value to the cell. This raster layer was used to estimate zonal statistics (minority and majority/mode values) and characterise each land cover class in order to define their potential management type. These analyses were carried out in ArcGIS 10.4.1®.

4.3 Results

4.3.1 GPP response to limiting factors per land cover class

In the time frame 2000-2010, the lowest GPP values were found in the class grasslands with median values varying around 0.5 kg C/m^2. In croplands, GPP reached median values ca. 1.1 kg C/m^2. The highest values of GPP were found in croplands/natural vegetation mosaic with median values fluctuating around 1.4 kg C/m^2 (Figure 4.2). The number of samples per land cover class was between 2066 and 3370 after excluding duplicates for all the variables as well as those values below Cook’s distance threshold (Table 4.2).

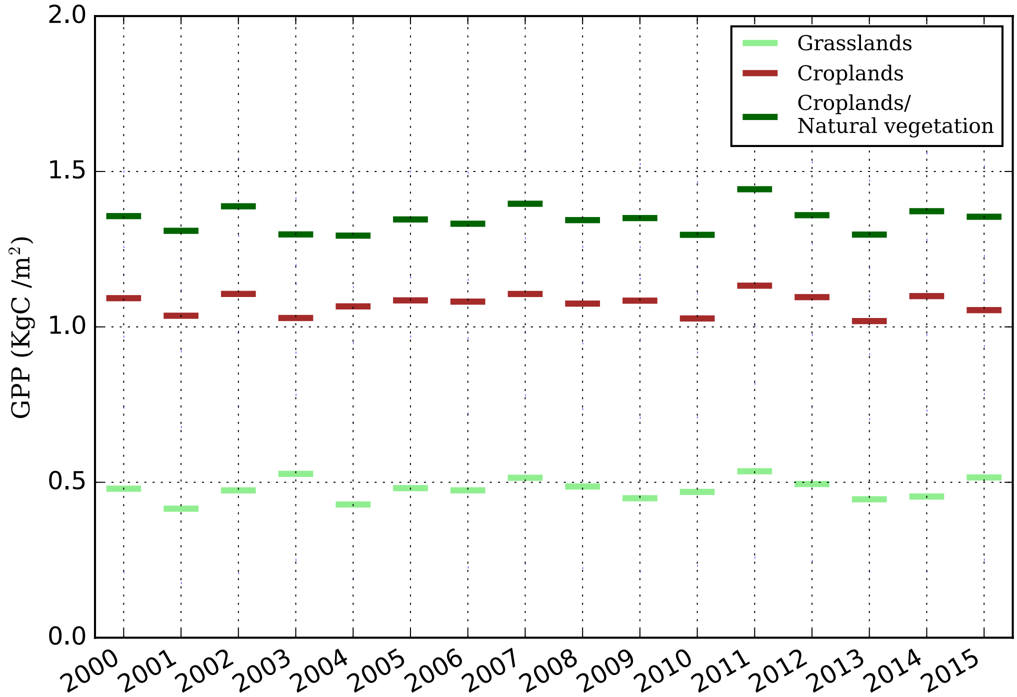

Figure 4.2. GPP median values per year and land cover class.

Table 4.2 Number of samples (n) of all the variables (GPP, N deposition, temperature, precipitation, and sunshine) with unique values and influential values and outliers excluded. Class 10: grasslands, class 12: croplands, and class 14: croplands/natural vegetation mosaic.

Year	2000			2007			2010		
Class	10	12	14	10	12	14	10	12	14
n	2988	2066	3327	2978	2074	3370	2965	2074	3346

The highest correlations were found between GPP and N deposition and between GPP and temperature. The lowest correlations were found between GPP and precipitation. In particular, very low or no correlation between both variables were found in 2007 and 2010 for grasslands (≈0.1 and ≈-0.04 respectively) and croplands/natural vegetation mosaic (≈0.1 and -0.04) (Figure 4.3 and Supporting information Table S1).

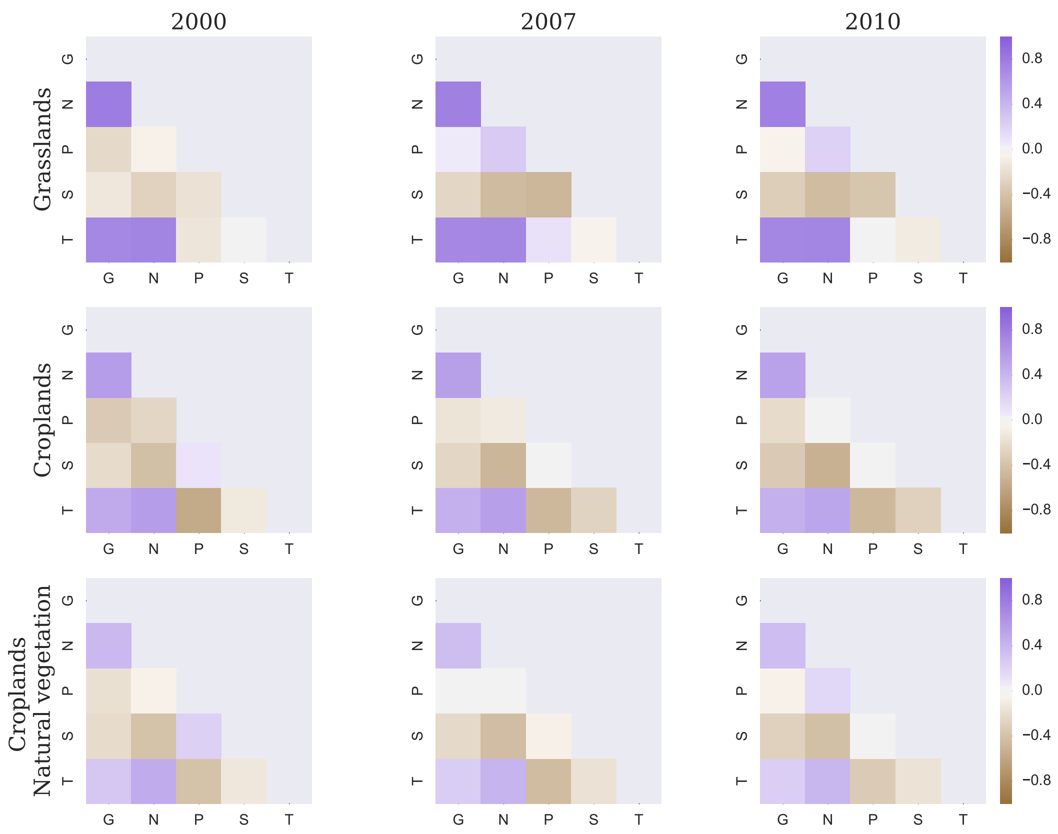

Figure 4.3 Correlation matrix between the dependent and independent variables per year and land cover class with no duplicates. G: GPP, N: N deposition, P: Precipitation, S: Sunshine, and T: Temperature.

4.3.1.1 Grasslands

All independent variables showed a linear relationship with the dependent variables except for N deposition. Therefore, this variable was transformed for all the years with a natural logarithm to improve linearity with GPP. The two variables that mostly explained the variance of GPP were N deposition and precipitation (Table 4.3).

Table 4.3 Coefficient of determination (R^2) change per variable (alphabetically ordered) that the stepwise regression model selected for grassland.

	2000	2007	2010
	R^2 change	R^2 change	R^2 change
N deposition	67.7 %	63.7 %	66.0 %
Precipitation	8.1 %	9.5 %	13.6 %
Sunshine	0.5 %	0.1 %	0.3 %
Temperature	0.2 %	1.4 %	0.2 %

Table 4.4 Order of variables entered into the model and adjusted R^2 according to the addition of a new variable to the model: N deposition: N dep, temperature: Temp, precipitation: Precip, and sunshine: Sunsh. **Statistically significant $p < 0.01$.

2000			2007			2010		
Order	Adjusted R^2	RMSE	Order	Adjusted R^2	RMSE	Order	Adjusted R^2	RMSE
N dep	.677**	.225	N dep	.637**	.246	N dep	.660**	.220
Precip	.759**	.194	Precip	.731**	.212	Precip	.796**	.171
Sunsh	.764**	.192	Temp	.746**	.206	Temp	.798**	.170
Temp	.766**	.191	Sunsh	.747**	.206	Sunsh	.800**	.169

Pearson's correlations showed that N deposition and temperature were the variables higher correlated to GPP (Figure 4.3 and Supporting information Table S1). The values of collinearity for the model that obtained the lowest RMSE achieved (including all explanatory variables) 0.23 for T and 4.5 for VIF. The addition of variables to the ones already in the model (e.g. model 1: N deposition, model 2: N deposition and precipitation, etc.) increased the coefficient of determination (R^2) up to 0.77 in 2000, 0.75 in 2007, and 0.8 in 2010 (

Table 4.4).

Standardized residuals were normal distributed in all the cases. D-W values from 1.9 to 2 indicated independence of residuals, and the B-P test showed residuals with heteroscedasticity statistically significant. The leave-one-out cross-validation resulted in SR R^2 values ca. 0.9 for all the years. The regression coefficients to build the model for statistical inference are shown in Table S2 (Supporting information).

4.3.1.2 Croplands

A natural logarithmic transformation was applied only for N deposition in the dataset from 2000 because the remaining independent variables showed a linear relationship with the dependent variable for 2007 and 2010. N deposition was the independent variable that influenced the most on the GPP response. Precipitation followed N deposition in relevance for the years 2000 and 2010. However in 2007, temperature was the variable that followed N deposition in importance and the remaining variables were excluded from the model (Table 4.5).

Table 4.5 Coefficient of determination (R^2) change per variable (alphabetically ordered) that the stepwise regression model selected for croplands.

	2000	2007	2010
	R^2 change	R^2 change	R^2 change
N deposition	44.1%	37.9 %	34.6 %
Precipitation	2.7 %	Excluded	5.0 %
Sunshine	0.2 %	Excluded	0.7 %
Temperature	Excluded	2.4 %	0.6 %

N deposition and temperature were the independent variables more correlated to GPP in all the years (Figure 4.3 and Supporting information Table S1). However, correlation between these variables resulted either in exclusion of the one less correlated to GPP or later addition to the model. The final model achieved collinearity statistics between 0.49 and 0.88 for T and between 1.14 and 2.06 for VIF. The explanatory variables reached adjusted R^2 values ca. 0.4 (Table 4.6).

Table 4.6 Order of variables entered into the model and adjusted R^2 according to the addition of a new variable to the model: N deposition: N dep, temperature: Temp, precipitation: Precip, and sunshine: Sunsh. Variable excluded from the model: Excl. **Statistically significant $p < 0.01$.

2000			2007			2010		
Order	Adjusted R^2	RMSE	Order	Adjusted R^2	RMSE	Order	Adjusted R^2	RMSE
N dep	.441**	.194	N dep	.378**	.212	N dep	.346**	.211
Precip	.468**	.190	Temp	.402**	.207	Precip	.395**	.203
Sunsh	.470**	.189	Precip	Excl		Sunsh	.402**	.202
Temp	Excl		Sunsh	Excl		Temp	.408**	.201

Standardized residuals were normal distributed for all the datasets. D-W values were ca. 1.9 revealing independence of errors. The B-P test showed heteroscedasticity statistically significant. The leave-one-out cross-validation resulted in SR R^2 values ca. 0.6 for all the years. The regression coefficients to create the model for statistical inference are shown in Table S2 (Supporting information).

4.3.1.3 Croplands/natural vegetation mosaic

All the explanatory variables presented a linear relationship with the dependent variable. N deposition largely explained the GPP response followed by precipitation in the years 2000 and 2007, and sunshine in 2010 (Table 4.7).

Table 4.7 Coefficient of determination (R^2) change per variable (alphabetically ordered) that the stepwise regression model selected for croplands/natural vegetation mosaic.

	2000	2007	2010
	R^2 change	R^2 change	R^2 change
N deposition	16.9 %	14.1 %	14.2%
Precipitation	2.1 %	1.4 %	1.0 %
Sunshine	Excluded	0.3 %	2.9 %
Temperature	Excluded	0.5 %	Excluded

The explanatory variables that reached high correlation with GPP were N deposition followed by positive correlations with temperature and negative correlations with sunshine (Figure 4.3 and Supporting information Table S1). The model with the lowest RMSE achieved values between 0.61 and 0.99 for T and 1 and 1.6 for VIF. Adjusted R^2 values reached ca. 0.18 in 2000 and 2010, and 0.16 in 2007 (Table 4.8).

Table 4.8 Order of variables entered into the model and adjusted R^2 according to the addition of a new variable to the model: N deposition: N dep, temperature: Temp, precipitation: Precip, and sunshine: Sunsh. Variable excluded from the model: Excl. **Statistically significant $p< 0.01$.

2000			2007			2010		
Order	Adjusted R^2	RMSE	Order	Adjusted R^2	RMSE	Order	Adjusted R^2	RMSE
N dep	.169**	.228	N dep	.141**	.247	N dep	.142**	.238
Precip	.189**	.225	Temp	.146**	.246	Sunsh	.171**	.234
Sunsh	Excl		Precip	.160**	.244	Precip	.181**	.232
Temp	Excl		Sunsh	.163**	.243	Temp	Excl	

Standardized residuals were not normal distributed in all samples. D-W values ca. 1.8 showed independence of errors. The K test indicated heteroscedasticity statistically significant. The leave-one-out cross-validation resulted in SR R^2 values ca. 0.4 for all the years. The regression coefficients to generate the model for statistical inference are shown in Table S2 (Supporting information).

4.3.2 Soil characteristics per land cover class

The zonal-statistics analysis using the digital soil suitability map characterised the aptitude for croplands, stone content, and water and nutrient storage capacity of the three land cover classes. The results indicated that the land cover class grasslands was mostly located in areas inappropriate for agriculture. The majority of the values of this land cover class with regard to stone content and water and nutrient storage capacity resulted in the category unknown. However, the minority of grasslands values were found in not stony areas with very good nutrient and water storage capacity. Croplands were mainly placed in areas with very good aptitude for agriculture production, slightly stony, and with good water and nutrient storage capacity. Croplands/natural vegetation mosaic were mostly characteristic of stony areas inappropriate for agriculture, with good water and nutrient storage capacity.

4.4 Discussion

4.4.1 GPP response to limiting factors per land cover class

4.4.1.1 Land cover classes

The land cover product used in this study (MCD12Q1) is also used as input in the algorithm that retrieves GPP. Therefore, we stratified the analysis according to the MODIS land cover classes for consistency. The GPP algorithm is based on the UMD classification scheme proposed by the University of Maryland. However, we used the IGBP legend in which the UMD class croplands is divided in two classes: croplands and croplands/natural vegetation mosaic. Friedl et al. (2010) reported an overall accuracy of 74.8% for the MCD12Q1 product using the IGBP legend.

The N deposition model uses as input the Swiss Land-Use Statistics grid (FSO, 2005). In particular, this model differentiates between croplands and grasslands, and alpine meadows and pastures. The former two classes located in the Midlands and the Jura mountains can be related to the MCD12Q1 selected classes: croplands and croplands/natural vegetation mosaic respectively. The latter two classes located in the alpine region can be linked to the MCD12Q1 class grasslands.

In general terms, we could consider the classes croplands and croplands/natural vegetation mosaic as land cover classes with intensive management practices. The class grasslands, mostly located in the alpine region, could be defined as areas with extensive management practices. Nevertheless, the class croplands/natural vegetation mosaic is mainly located in areas inappropriate for agricultural production (Section 4.3.2). Therefore management practices in croplands/natural vegetation mosaic could be not as intensive as in the class croplands located in areas with very good aptitude for agricultural use.

On the other hand, the three land cover classes can be found at low altitude (ca. 200 m a.s.l., Section 4.2.1). Therefore, different levels of intensity are expected in all of them, especially in the class cropland/natural vegetation mosaic because the area is most likely used as intensively managed grassland systems. All in all, taking into account the results obtained, we considered three management types: high intensive management (croplands), medium intensive management (croplands/natural vegetation mosaic), and low intensive management (grasslands).

4.4.1.2 GPP response to limiting factors

The highest GPP values can be reached in heterogeneous floristic areas with medium management practices (croplands/natural vegetation mosaic), followed by areas with high management practices (croplands), and low managed areas (grasslands) (Figure 4.2).

N deposition achieved higher predictive power of GPP response than climatic factors in all the land cover classes. From the selected climatic variables, precipitation was relevant to generating the models due to correlation between N deposition and temperature —such a correlation was also found by Maskell et al. (2010)— as well as between other variables that increased collinearity (Figure 4.3). Nevertheless, the influence of N deposition and precipitation varied among land cover classes. The selected explanatory variables would explain up to 80% the GPP response using the grasslands population data to generate a regression model. However, the explanatory performance of these variables would decrease to relative maximums of 47% in croplands, and 19% in croplands/natural vegetation mosaic. The regression equations generated from the samples would predict the GPP response using the population data of each land cover class with SR R^2= 0.9 in grasslands, SR R^2= 0.6 in croplands, and SR R^2= 0.4 in croplands/natural vegetation mosaic.

In grasslands, N deposition and precipitation achieved higher influence on the GPP response than in croplands and croplands/natural vegetation mosaic. At higher altitudes, C and N soil inputs decrease because of high soil permeability and low temperatures (Hitz et al., 2001). Therefore, addition of basic nutrients such as N and water is key to enhance photosynthetic activity. N deposition was the most relevant variable overtaking the predictive power of precipitation by 55%. Stevens et al. (2015) also obtained better predictive results of grasslands productivity using N deposition as explanatory variable at a global scale.

In croplands, N deposition reached similar values for all the years explaining 39% average of GPP variance. Nevertheless, N deposition reduced its explanatory power by half with respect to grasslands. Precipitation and temperature played similarly a small role in terms of influence on GPP response (from 2.4% to 5%). This land cover class is managed and located in areas with good water and nutrient storage capacity. Furthermore, legume-based crops (grassland in rotation) that reach high rates of N inputs by means of N_2 fixation can maintain a moderate-high level of productivity in the long-term (Ledgard, 2001). Therefore, N deposition could have less relevance in these productive croplands than in grasslands located in the alpine region.

In croplands/natural vegetation mosaic, N deposition achieved the lowest predictive performance of GPP as compared with the classes grasslands and croplands. Apart from the potential influence of legume-based crops on productivity aforementioned, Bassin, Volk, Sutter, et al. (2007) showed that N deposition could enhance, diminish or not affect productivity of certain species in rich plant communities. Therefore, the low influence of N deposition in GPP response could be explained by complex biosphere-atmosphere interactions; these interactions can also trigger changes in plant species (Bassin et al., 2013; Schuster et al., 2016; Vankoughnett et al., 2014). Abiotic and biotic factors mediate N deposition effects in terrestrial ecosystems producing different impacts among biomes (Matson et al., 2002). Additionally, part of the class croplands/natural vegetation mosaic is located in the Jura mountains receiving less sunshine as compared with the class croplands. The influence of this region could explain that sunshine overtook precipitation in relevance as limiting factor in 2010.

4.4.2 Implications of high N deposition in low, medium, and highly managed ecosystems

The highest effect of N deposition on the GPP response was observed in the class grasslands, which is mostly located in the alpine biogeographic region. In areas with low nutrient inputs, productivity can be enhanced via N deposition. However, global model projections reveal N deposition as the third driver with the largest impact on biodiversity in alpine areas (Sala et al., 2000). Therefore, further attention should be paid to the effects of atmospheric N in alpine grasslands. In medium managed areas with high plant species richness (croplands/natural vegetation mosaic) the impact of N deposition observed on GPP response was the least (Section 4.3.1.3). However, in intensively used areas it has been recommended including atmospheric N inputs in nutrient balance of agroecosystems (He et al., 2010). In addition, high N inputs through animal manure and mineral fertilizer are common in croplands leading to nutrient leaching and eutrophication of surface waters (Bergström et al., 2006; Camargo et al., 2006; Krupa, 2003).

4.4.3 N deposition and C budget models

The relevance of N deposition as controlling factor of GPP response as well as the interactions observed between factors can help understand the predictive performance of these variables in regions with diverse land management practices. A recent simulation of GPP dynamics in an alpine dry meadow indicated that climatic factors reached a predominant influence on GPP over the growing season i.e. soil moisture > temperature > N deposition (Fan et al., 2016). Nevertheless, the correlation between climatic factors and GPP shown in our study are in line with the results of Beer et al. (2010) for Switzerland. Therefore, the comparison of analyses carried out in areas with different climatic conditions and land management practices contribute to understanding the relevance of precipitation, temperature, sunshine, and N deposition on C fixation. Besides, these findings can foster the inclusion of N deposition estimates in future global

C budget analyses, which have been mostly focused on climatic variables (Beer et al., 2010; Zhang et al., 2014), in particular, temperature (Verstraeten et al., 2006). Some efforts have started to be made at a regional scale (Schulze et al., 2010) and at specific biomes such as grasslands (Stevens et al., 2015). The results of our analysis indicate that the relevance of climatic variables could be shifted after including other explanatory variables such as N deposition and further inclusion of this variable in C budget models.

4.5 Conclusions

Remote sensing GPP products captured the influence of N deposition, precipitation, relative sunshine, and temperature on the C fixation response of three land cover classes with different management types. The highest GPP response was found in rich plant communities with medium management practices (croplands/natural vegetation mosaic), followed by highly managed (croplands), and low managed areas (grasslands). The results of the multiple regression analyses showed that N deposition was the variable that mostly predicts GPP response in all the land cover classes. Nevertheless, the predictive performance of N deposition varied with the land cover classes reaching the best results in grasslands, followed by croplands, and croplands/natural vegetation mosaic. The most relevant climatic variable for all the models was precipitation with occasional relevance of temperature and sunshine in specific years. The selected variables would mostly explain GPP variance in grasslands population data. Finally, we suggested monitoring the long-term impact of N deposition on the composition of plant species in areas with high plant diversity such as alpine grasslands.

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Supporting information

Table S1 Pearson's correlation between GPP and the N deposition (N dep), temperature (Temp), precipitation (Precip), and sunshine (Sunsh) based on a bootstrap of 1000 samples per land cover class and year. **Statistically significant p< 0.01.

Grasslands

	GPP 2000		GPP 2007		GPP 2010	
	Pearson correlation	95% CI	Pearson correlation	95% CI	Pearson correlation	95% CI
N dep	.823** ± .006	.811— .833	.798** ± .006	.786 — .811	.813** ± .006	.801 — .824
Temp	.741** ± .008	.724 — .756	.749** ± .008	.734 — .763	.748** ± .008	.733 — .763
Precip	-.220** ± .016	-.250 — -.190	.059** ± .017	.026 — .092	-.035** ± .017	-.069 — -.001
Sunsh	-.121** ± .019	-.158 — -.086	-.233** ± .018	-.270 — -.197	-.291** ± .018	-.325 — -.256

Croplands

	GPP 2000		GPP 2007		GPP 2010	
	Pearson correlation	95% CI	Pearson correlation	95% CI	Pearson correlation	95% CI
N dep	.664** ± .011	.643 — .687	.615** ± .013	.590 — .640	.588** ± .013	.560 — .616
Temp	.527** ± .015	.499 — .554	.487** ± .016	.455 — .518	.477** ± .016	.445 — .508
Precip	-.383** ± .018	-.418 — -.347	-.164** ± .023	-.208 — -.115	-.236** ± .021	-.276 — -.195
Sunsh	-.243** ± .018	-.278 — -.207	-.307** ± .019	-.346 — -.268	-.387** ± .016	-.419 — -.357

	Croplands/ Natural vegetation mosaic					
	GPP 2000		GPP 2007		GPP 2010	
	Pearson correlation	95% CI	Pearson correlation	95% CI	Pearson correlation	95% CI
N dep	.411** ± .013	.384 — .438	.375** ± .014	.349 — .405	.377** ± .014	.349 — .405
Temp	.245** ± .017	.212 — .277	.220 ** ± .017	.187 — .253	.192** ± .017	.160 — .226
Precip	-.173** ± .016	-.202 — -.141	.068** ± .016	.037 — .100	-.040** ± .016	-.074 — -.008
Sunsh	-.215** ± .014	-.244 — -.186	-.229** ± .015	-.259 — -.198	-.320** ± .014	-.348 — -.293

Table S2 Regression coefficients with heteroscedasticity-consistent standard errors per land cover class and year. Const: Constante, N deposition: N dep, temperature: Temp, precipitation: Precip, and sunshine: Sunsh. *Statistically significant p< 0.05. **Statistically significant p< 0.01.

	Grasslands					
	2000		2007		2010	
	Coefficients	95% CI	Coefficients	95% CI	Coefficients	95% CI
Const	-.8075** ± .0704	-.9456 – -.6695	.1089 ± .0971	-.0815 – .2994	.0783 – .0587	-.0367 – .1934
N dep	.6270** ± .0121	.6033 – .6507	.5469** ± .0136	.5201 – .5736	.6095* ± .0119	.5862 – .6329
Precip	-.0002** ± .0000	—	-.0003** ± .0000	—	-.0003** ± .0000	—
Sunsh	.0075** ± .0013	.0051 – .0100	-.0057** ± .0016	-.0088 – -.0026	-.0066** ± .0010	-.0086 – - .0047
Temp	.0103** ± .0018	.0068 – .0139	.0279** ± .0020	.0240 – .0319	.0123** ± .0016	.0091 – .0155

	Croplands					
	2000		2007		2010	
	Coefficients	95% CI	Coefficients	95% CI	Coefficients	95% CI
Const	-.1581* ± .0783	-.3116– -.0046	.5791** ± .0123	.5549 – .6033	1.018** ± .0540	.9123– 1.124
N dep	.4115** ± .0114	.3891 – .4338	.0197** ± .0008	.0181 – .0212	.0185** ± .0009	.0168– .0203
Precip	-.0001** ± .0000	—	—	—	-.0001** ± .0000	—
Sunsh	.004** ± .0012	.0017 – .0064	—	—	-.0062** ± .0011	-.0083 – -.0042
Temp	—	—	.0192** ± .0017	.0158 – .0226	.0104** ± .0017	.0070 – .0138

	Croplands/Natural vegetation mosaic					
	2000		2007		2010	
	Coefficients	95% CI	Coefficients	95% CI	Coefficients	95% CI
Const	1.077** ± .0175	1.042 – 1.111	.9787** ± .0643	.8527 – 1.1048	1.568** ± .0478	1.475 – 1.662
N dep	.0167** ± .0006	.0154 – .0179	.0123** ± .0008	.0107 – .0138	.0138** ± .0007	.0123 – .0152
Precip	-.0001** ± .0000	—	.0001** ± .0000	—	-.0001** ± .0000	—
Sunsh	—	—	-.0041** ± .0010	-.0061 – -.0021	-.0120** ± .0010	-.0139 – -.0101
Temp	—	—	.0205** ± .0022	.0161 – .0248	—	—